Why breed every other year? The case of albatrosses

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Albatrosses exhibit extremely low reproductive rates, each pair brooding only one egg and subsequent chick at a time. Furthermore, in several of the species, the majority of successful pairs breed only once every second year (termed 'biennial' breeding). Thus, on average, these latter species have an annual fecundity of about half an offspring per year, while other albatrosses produce an egg and chick every year. Using our 40-year bank of demographic data, we compared 12 species of albatrosses according to these two breeding strategies to examine potential causes of biennial breeding. Biennial breeding could be due to physiological constraints, larger animals breeding more slowly, or ecological constraints, more distant pelagic feeding trips being energetically costly, or both. We tested these hypotheses by looking for predicted associations between the duration of the rearing period, the distance to the oceanic feeding zone and breeding frequency. We also looked for associations of these variables with other life-history traits. Body size had a strong influence on the duration of the rearing period, but not on the distance that birds travelled to the feeding zone. Both the duration of the rearing period and distance to the feeding zone appeared to have direct influences on breeding frequency, as revealed by a path analysis, and thus both hypotheses to explain biennial breeding were supported. Finally, breeding frequency exhibited a strong trade-off with adult survival and age at maturity, indicating that slower breeders live through more breeding seasons, perhaps mitigating their lower annual reproductive output.

Keywords: albatrosses; biennial breeding; life histories; trade-offs

1. INTRODUCTION

Albatrosses (family Diomedidae, order Procellariiformes) are textbook examples of species with low reproductive rates and long lives (Stearns 1992). Albatrosses are unusual because pairs care for only one egg or chick during a breeding season, without laying a replacement egg if they fail (Tickell 2000). Also, albatrosses are very large birds, with body mass of species ranging from *ca.* 2 to 9 kg (Jouventin & Mougin 1981). All albatross species are pelagic, although their offshore foraging zones vary in distance from the breeding colony. These species also have extremely long lifespans: up to at least 51 years in Buller's albatross, *Thalassarche bulleri*; and 64 years for a female Royal albatross, *Diomedea epomophora* (64 years of breeding, and because the mean age at maturity is 10 years, she was probably 74! (Del Hoyo *et al.* 1992; Sagar & Warham 1993). In addition, in some species, most pairs brood an egg and chick only every other year, and thus are biennial breeders (Tickell 2000). Reproductive failure can be followed by a one-year period, while a pair waits to breed again. Because some adult pairs fail to breed, a scale of average annual fecundity occurs, varying from about half an egg per year in biennial breeders to almost an egg per year in some annual breeders.

Biennial breeding is unusual among animal species, but not in albatrosses. Thus, albatrosses provide a good opportunity for studying extreme life histories in species that are similar in their lifestyles. There are five species of

albatross in which pairs, on average, breed every other year. A good example is the wandering albatross, *Diomedea exulans*, the largest seabird and one of the best-studied biennial breeders (Tickell 1968; Jouventin & Weimerskirch 1988; Weimerskirch & Jouventin 1987). Another species, the grey-headed albatross, *Thalassarche chrysotoma*, has some pairs that breed biennially, while others breed annually (Tickell & Pinder 1967). Finally, there are about eight species in which most pairs breed every year. We estimated the frequency of reproduction for 12 of the albatross species, including all of the biennial breeders, and compared annual and biennial species with respect to ecological and life-history characteristics, in order to test two hypotheses that might explain the evolutionary shift to biennial breeding.

The first hypothesis to explain biennial breeding is that because albatrosses are extremely large birds, development of chicks from incubation to brooding to fledging may take longer, because growth to a larger size can require more time. In addition to the length of the rearing period, adults have to spend further time and energy molting before the next breeding bout can take place. Biennial breeding would be mandated if rearing, molting and recovery of body condition needed for breeding takes more than a year. Thus, we expect larger species to have a longer rearing period, and a longer rearing period should be associated with biennial breeding. This idea was previously suggested as a partial explanation of biennial breeding in albatrosses, but sampled species were too few for statistical comparisons (Jouventin & Weimerskirch 1988). The second hypothesis is that birds that have to travel further to forage might have relatively slower cycles

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of reproduction (Lack 1968; Jouventin & Mougin 1981; Jouventin & Weimerskirch 1988). This could occur due to the direct effect of slowed or poor resource accumulation by birds that have to travel further to forage, and/or indirectly due to an influence of the foraging distance on the duration of the rearing period. Of course, we might also expect larger species to be able to forage at greater distances from the breeding grounds. Thus, there is considerable overlap between the hypotheses. Nonetheless, opportunities to reject one or both of the alternatives could occur in an interspecific comparison of the albatross species.

We examined an extensive dataset on 12 of the 14 (16) albatross species. Many of the data were collected over a period of up to 40 years of field observations, and we added literature sources to our unpublished data. For the 12 species, we looked for evidence that would allow us to confirm or reject either or both of our two alternative hypotheses. In addition, we looked for any potential influence of biennial breeding on the exceptionally high adult survival rate exhibited by all albatross species. While we realize that, theoretically, reproduction and survival should have a negative association, and thus are likely to coevolve, we also recognize that any constraints on reproduction could have associated influences on patterns of survival. Our general expectation was that slower breeders should have longer lifespans relative to species in which breeding is primarily annual. Because a phylogeny was available for the species (Nunn *et al.* 1996), we performed our analyses both with and without adjusting the data for phylogeny (Price 1997).

2. METHODS

Several populations of albatrosses were banded annually for estimates of reproduction and survival, with some species monitored for up to 40 years (Anderson 1979; Serenty & Curry 1983; Jouventin *et al.* 1984; Croxall & Rothery 1991). We collected the results of such studies from the literature, and from our 40-year bank of data on several of the species (see Appendix A). The following data were collected for each species: body mass of adult females, average annual adult survival, age at first breeding, duration of incubation shift (males and female take turns incubating, and this is the mean time that each sits before being relieved by the partner), the average number of feeding visits per day during the period before fledging (both parents feed the chick on the nest during this time), duration of incubation and rearing (added together to produce the duration of the rearing period), average fledging success, a class variable for the distance of the foraging zone from the breeding colony (1, 'coastal' (foraging range less than 200 km offshore); 2, 'pelagic' (foraging range more than 200 km and less than 1000 km); or 3, 'highly pelagic' (foraging range more than 1000 km)) and frequency of breeding (annual rate of production of an egg). The pelagic range of several species is not still known, but we combined measurements obtained by satellite tracking (Jouventin & Weimerskirch 1990) and observations at sea of banded birds into a class variable. Because pairs lay only one egg, the mean frequency of breeding was the best measure of reproductive rate for interspecific comparisons (Allaine *et al.* 1987).

In each of the reviewed studies, the different parameters were not always collected and summarized in the same way. In addition, some variables, such as the duration of brooding turns

that partners take, change as the reproductive season progresses (Weimerskirch *et al.* 1993; Weimerskirch 1995). In these cases, we took the conservative approach of deleting any questionable data. We examined natural-log transformations of variables measured in grams, days, years, and number of young, and arcsine- and natural-log-transformed frequencies (Gaillard *et al.* 1989). Transformations, however, did not improve normality of the variables, as the fit to a normal distribution was much poorer in some cases, and both sets of analyses were identical in pattern. Thus, we conducted analyses on untransformed data.

We first examined differences between annual and biennial breeding species (six species in each group) with ANOVA. For the analyses, we considered grey-headed albatrosses as exhibiting biennial breeding, although some pairs breed annually. We then examined correlations among variables that differed between these two groups of species. We constructed a 'flow' diagram of how the two hypotheses might interact and how they might influence breeding frequency (after Jouventin & Weimerskirch 1988). As part of this diagram, we conducted a standardized partial regression analysis (*viz.*, path analysis) to evaluate direct and indirect influences of the duration of the rearing period and distance to the feeding zone on breeding frequency.

We used a phylogeny for the albatrosses' family (Diomedidae) that was derived from cytochrome-*b* data (Nunn *et al.* 1996). In the absence of reliable branch lengths for the species, we assumed equal amounts of time between adjacent nodes on the tree. Phylogenetic influences on variation in life-history traits among albatross species were estimated by network autocorrelation (after Cheverud *et al.* 1985; Dunham & Miles 1992). Values of r^2 from network autocorrelation analyses were used to indicate whether there was 'phylogenetic signal' in our variables. We further examined phylogenetically independent contrasts (after Felsenstein 1985), using the PDAP software (Garland *et al.* 1999; Garland & Ives 2000). Statistical analyses were preformed using SAS (SAS Institute, Inc. 1990) and Microsoft EXCEL, v. 5.0.

3. RESULTS

We first looked for differences between species that exhibit primarily annual breeding versus those that exhibit biennial breeding. Biennial breeders were not quite significantly larger than annual breeders (table 1), primarily because the two species of sooty albatrosses are biennial breeders, but are among the smallest albatrosses (Jouventin & Weimerskirch 1988). Biennial breeders survived better than annual breeders, although only by *ca.* 2%. Biennial breeders also had a later age at maturity, shorter shifts of partners during incubation, a longer rearing period (defined as the period from laying to fledging) and more distant feeding zones than annual breeders. There was no difference, however, between annual and biennial breeders in the frequency of feeding of chicks during brooding or in fledging success.

Network autocorrelation revealed that among the life-history variables of albatrosses, phylogeny explained more than 10% of the variation in only body mass ($r^2 = 0.25$) and the length of the rearing period ($r^2 = 0.37$). Although perhaps substantial, these autocorrelations were not significant (all *z*-scores less than 1.33, $p > 0.18$). We performed correlation analyses of our variables both with unadjusted data and data adjusted for phylogeny by inde-

Table 1. Differences in average life-history traits for albatross species that primarily have annual breeding and species that exhibit biennial breeding.

(Sample sizes throughout are six annual breeders and six with biennial breeding.)

life-history traits	mean (± 1 s.d.) annual breeders	mean (± 1 s.d.) biennial breeders	<i>F</i>	<i>p</i>
body mass	3040 $\pm$ 598	5245 $\pm$ 2719	3.77	0.08
adult survival	0.931 $\pm$ 0.016	0.952 $\pm$ 0.015	5.66	0.04
age at maturity	9.03 $\pm$ 1.14	11.35 $\pm$ 1.26	11.14	0.01
incubation shift	13.16 $\pm$ 3.81	8.73 $\pm$ 1.91	6.49	0.03
feeding frequency	0.498 $\pm$ 0.155	0.500 $\pm$ 0.141	0.00	0.98
rearing period	212.7 $\pm$ 20.8	280.7 $\pm$ 63.9	6.14	0.03
fledging success	0.503 $\pm$ 0.183	0.552 $\pm$ 0.377	0.25	0.62
feeding zone	1.833 $\pm$ 0.753	2.833 $\pm$ 0.408	8.18	0.02
breeding frequency	0.845 $\pm$ 0.045	0.540 $\pm$ 0.040	153.34	0.0001

Table 2. Correlations of life-history traits of 12 species of albatrosses.

(For individual two-tailed tests: $\alpha < 0.05$ for $r = 0.576$; and $\alpha < 0.01$ for $r = 0.708$. Below the diagonal, correlations of phylogenetically independent contrasts of life-history traits; after Felsenstein (1985).)

	body mass (g)	adult survival	age at maturity (years)	incubation shift (days)	rearing period (days)	feeding zone	breeding frequency
body mass	—	0.037	0.099	-0.475	0.901	0.279	-0.621
adult survival	-0.181	—	0.347	0.061	0.258	0.430	-0.599
age at maturity	0.299	0.338	—	-0.524	0.056	0.353	-0.640
incubation shift	-0.451	0.151	-0.468	—	-0.496	-0.278	0.646
rearing period	0.821	0.050	0.131	-0.477	—	0.486	-0.700
feeding zone	0.136	0.380	0.255	-0.167	0.535	—	-0.646
breeding frequency	-0.487	-0.560	-0.714	0.603	-0.593	-0.576	—

pendent contrasts (table 2). Because the direction of correlations among variables and the general magnitude of correlations were similar, we concluded that phylogenetic influences were not substantial. In such circumstances, making adjustments for phylogeny might be as likely to obscure patterns as reveal them (Price 1997), so we chose to conduct further analyses on unadjusted data.

We examined correlations among variables that differed between annual and biennial breeding albatrosses. Body mass was most strongly associated with the length of the rearing period (figure 1), and secondarily and negatively with mean breeding frequency (table 2). Mean breeding frequency exhibited negative associations with traits associated with longevity (adult survival and age at maturity), positively with incubation shift, and negatively with the duration of the rearing period and the rank distance to the feeding zone.

We examined these associations within the context of a diagram that reflected our expectations of associations of life-history traits under our two hypotheses to explain biennial breeding. Following our expectation from the first hypothesis, body mass was positively correlated with the length of the rearing period, but body mass had little association with the distance to the feeding zone (figure 2). Because the length of the rearing period, distance to the feeding zone and breeding frequency all exhibited strong associations, we conducted a path analysis of these three variables.

Multiple regression indicated that the length of the rearing period and distance to the feeding zone could account

Figure 1. For 12 species of albatrosses, the association of the length of the rearing period (incubation and gestation combined) and adult body mass. Annual breeders are indicated by diamonds and biennial breeders by triangles ($r^2 = 0.81$, $F = 43.0$, $p < 0.0001$).

for the majority of variation in the frequency of reproduction ($r^2 = 0.613$, d.f. = 2,9, $F = 7.12$, $p = 0.01$). As expected under the first hypothesis, rearing period appeared to have a significant negative path to breeding frequency (figure 1; $p = -0.505$, $t = -2.127$, one-tailed $p = 0.03$). As expected under the second hypothesis, the feeding zone had a negative path to breeding frequency that approached significance ($p = -0.401$, $t = -1.691$, one-tailed $p = 0.06$). The length of the rearing period and

body mass

Figure 2. A flow diagram of life-history traits of albatrosses reflecting two hypothesized influences on breeding frequency (viz., that it is slowed by lengthy rearing periods and that it is slowed for species with feeding zones far from the breeding colonies). Path coefficients (p -values) for a path analysis (viz., a standardized partial regression analysis) are given for the regression of breeding frequency on rearing period and feeding zone. All other associations (r -values) are measured by correlation. (Single asterisk, significance at the $\alpha = 0.05$ level; and double asterisk, significance at the $\alpha = 0.01$ level.)

feeding zone, however, were positively associated, so bias may have occurred due to collinearity. Collinearity causes two problems: inflation of the path coefficients and inflation of the variance about these coefficients. Our maximum condition index of 11.3 indicated that some inflation of the path coefficients probably occurred, although some authors indicate that the index must be over 30 to indicate a serious problem (Petraitis *et al.* 1996). Thus, we present both the path coefficients (figure 2) and correlations among the variables (table 2). Variance inflation factors for our path coefficients were both 1.31, well below the recommended cut-off value of 10 (Myers 1990).

Finally, we considered whether the life histories of albatrosses reflected an expected trade-off between reproduction and survival (Reznick 1985). Because fledging success did not vary between annual and biennial breeders (table 1), albatrosses lay only one egg per breeding season (see § 1), and breeding frequency exhibited strong associations with other life-history traits, we chose to examine the latter variable for comparison with variables that reflected longevity. Breeding frequency was significantly negatively associated with adult survival and with age at maturity (figure 2).

4. DISCUSSION

Our purpose was to test two hypotheses about possible causes of biennial breeding. We examined this in albatrosses because they comprise a sample of both annual and biennial breeding species in a single family of birds that exhibit similar lifestyles. In particular, albatrosses, like all Procellariiform species, lay only one egg per breeding

attempt (Warham 1990). Thus, breeding success should be closely allied to breeding frequency in these species, especially as fledging success was not significantly different between annual and biennial breeders (table 1).

Our first hypothesis was that the length of the rearing period for large albatrosses is simply too long for adults to recover body condition in time to breed in successive years. As expected, the length of the rearing period was strongly influenced by body mass, with the largest albatrosses having the longest rearing periods (figure 1). However, large size alone was not sufficient to explain biennial breeding, because the two sooty albatross species are biennial breeders (Appendix A; see also Jouventin & Weimerskirch 1988). Sooty albatrosses are among the smallest species in this group. However, the rearing period lasted on average almost 10 weeks longer in biennial breeders (table 1). Path analysis revealed a significant influence of rearing period on breeding frequency (figure 2), so this hypothesis was supported in albatrosses.

Our second hypothesis was that the distance to the feeding zone would limit breeding frequency, either directly or by influencing a longer rearing period. Lack (1968) first suggested the idea that long trips to distant foraging zones should reduce reproductive rates in pelagic feeding birds, although his prediction was for seabirds in general, rather than for a closely related group like albatrosses. Nonetheless, we examined this second hypothesis. We expected that body size might have an influence on how far birds foraged from the breeding colony, because larger birds might more easily cover thousands of kilometres of ocean. But body mass had little association with the distance to the feeding zone (table 1). However, there appeared to be a direct influence of the distance to the feeding zone on breeding frequency in albatrosses (figure 2). Also, because the distance to the feeding zone and the duration of the rearing period were correlated, an indirect influence was possible: of the feeding zone on breeding frequency through lengthened rearing periods for biennial breeders. The duration of incubation shifts was actually shorter in biennial breeders, but feeding rates of parents during brooding were very similar for annual versus biennial breeders. An indirect influence of feeding zone on the rearing period and then breeding frequency was not evident. The potential strength of an indirect effect can be estimated by the product of the correlation between the feeding zone and the rearing period multiplied by the path coefficient between the rearing period and breeding frequency. This estimate ($r \times p = -0.245$) was low, indicating that any indirect effect was slight, although the total effect of the feeding zone on breeding frequency was substantial (direct effect + indirect effect: $-0.401 + -0.245 = -0.646$).

Until recently (Jouventin & Weimerskirch 1990), it was impossible to know where and how far pelagic birds travelled to feed at sea. Several satellite tracking studies of albatrosses have now been carried out, and allow measurement of the foraging range of an increasing number of species. Even though direct measurements of foraging range have not been made for all albatross species, we found a relationship between the foraging range (through our classification of feeding 'zones') and breeding frequency. Albatrosses make remarkable foraging trips of thousands of kilometres. These long foraging trips may be due to necrophagous dietary habits, as in vultures and

condors. Distant foraging trips may incur high costs in energy or time, and prevent parents from rearing several chicks. In biennial breeders, the cost of distant foraging trips may substantially lower the body condition of parents after rearing, explaining why the small biennial albatrosses like sooties have to wait more than one year to breed again, even though the rearing period is only about eight months (Appendix A; Weimerskirch 1999; Weimerskirch *et al.* 2000).

Reproduction and survival are expected to trade-off in life histories, although phenotypic evidence of such trade-offs cannot be used to test this hypothesis (Reznick 1985). Nonetheless, breeding frequency had a strong trade-off with adult survival and age at maturity (figure 2) as previously found in terrestrial birds (data from Saether (1988), reanalysed in Bennet & Harvey (1988)). Biennial breeders survived *ca.* 2% better than annual breeders. Because survival rates are extremely high for albatrosses, a 2% advantage can translate into many more years of life and thus many more years of breeding, perhaps mitigating slower reproductive rates (Weimerskirch *et al.* 1987; Jouventin & Weimerskirch 1991). Albatrosses may be an especially good group to show such trade-offs, because of their limited reproductive effort (*viz.*, production of a sin-

gle egg that occurs each year or every other year, and without replacement if the egg is lost).

In summary, both our hypotheses are compatible and complementary explanations of biennial breeding in albatrosses. Albatrosses breed biennially in part due to their large size but also because of their pelagic way of life. Great albatrosses are necessarily biennial due to their size and associated long rearing periods, and due to their impressive feeding trips (Jouventin & Weimerskirch 1988, 1990). But sooty albatrosses probably breed every two years primarily due to their distant foraging trips for such relatively small albatrosses. Finally, production of young and adult survival appear closely linked in albatrosses, and further studies of albatrosses and petrels may yield important insights for life-history theory.

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APPENDIX A

species	body mass	adult survival	age at maturity	incubation shift	feeding frequency	incubation	brooding	fledging success	feeding zone	breeding frequency	references
<i>Diomedea exulans</i>	9600	0.931	10.80	8.3	0.39	79	278	0.725	3	0.510	Fressanges du Bost & Segonzac (1976), Stahl (1983), Weimerskirch (1992, 1998), Chastel (1995), J. Bried, D. Pontié and P. Jouventin (unpublished data)
<i>Diomedea amsterdamensis</i>	6270	0.966	10.10	7.5	0.46	79	261	0.706	3	0.510	Jouventin <i>et al.</i> (1989), Chastel (1995), J. Bried, D. Pontié and P. Jouventin (unpublished data)
<i>Diomedea epomophora</i>	6500	0.946	10.00	6.5	0.77	79	236	0.588	2	0.510	Tickell (1968), Marchant & Higgins (1990)
<i>Phoebastria fusca</i>	2600	0.950	13.20	8.5	0.47	71	164	0.517	3	0.600	Stahl (1983), Chastel (1995), Weimerskirch (1998)
<i>Phoebastria palpebrata</i>	2800	0.973	12.00	12.0	0.39	67	157	0.377	3	0.530	Stahl (1983), Chastel (1995), Weimerskirch (1998)
<i>Thalassarche chlororhynchos</i>	2100	0.932	9.10	12.5	0.33	71	115	0.307	1	0.900	Jouventin <i>et al.</i> (1983), Stahl (1983), Weimerskirch (1998)
<i>Thalassarche bulleri</i>	2700	0.913	8.00	10.8	0.42	69	167	0.575	3	0.870	Sagar & Weimerskirch (1996), Sagar & Warham (1998)

(Cont.)

species	body mass	adult survival	age at maturity	incubation shift	feeding frequency	incubation	brooding	fledging success	feeding zone	breeding frequency	references
<i>Thalassarche chrysostoma</i>	3700	0.947	12.00	9.6	0.52	72	141	0.397	3	0.580	Stahl (1983), Weimerskirch <i>et al.</i> (1988), Prince <i>et al.</i> (1994) Marchant & Higgins (1990), Chastel (1995), Weimerskirch (1998), J. Bried, D. Pontié and P. Jouventin (unpublished data) Nelson (1968), Harris (1973), Anderson <i>et al.</i> (1998) Frings & Frings (1961), Rice & Kenyon (1962), Fisher (1975), Gould & Hobbs (1993) Frings & Frings (1961), Rice & Kenyon (1962), Gould & Hobbs (1993), Cousins & Cooper (1999)
<i>Thalassarche melanophris</i>	3740	0.914	11.20	9.2	0.48	68	125	0.583	1	0.840	
<i>Phoebastria irrorata</i>	3500	0.950	8.30	20.2	0.40	60	167	0.240	2	0.875	
<i>Phoebastria immutabilis</i>	2900	0.947	8.60	14.0	0.75	64	165	0.625	2	0.800	
<i>Phoebastria nigripes</i>	3300	0.930	9.00	12.3	0.61	65	140	0.688	2	0.785	
mean	4143	0.942	9.94	11.0	0.50	70.3	176.3	0.527	2.3	0.693	
standard deviation	2202	0.018	2.17	3.69	0.14	6.2	53.0	0.161	0.8	0.164	

REFERENCES

Allainé, D., Pontier, D., Gaillard, J. M., Lebreton, J. D., Trouvilliez, J. & Clobert, J. 1987 The relationship between fecundity and adult body weight. *Oecologia* **73**, 478–480.

Anderson, D. J. 1979 A 28 year study of breeding fulmars *Fulmarus glacialis* in Orkney. *Ibis* **121**, 293–300.

Anderson, D. J., Schwandt, A. J. & Douglas, H. D. 1998 Foraging ranges of waved albatrosses in the eastern tropical Pacific Ocean. In *The albatross biology and conservation* (ed. G. Robertson & R. Gales), pp. 180–185. Chipping Norton, UK: Beatty and Sons.

Bennet, P. M. & Harvey, P. H. 1988 How fecundity balances mortality in birds. *Nature* **333**, 216.

Chastel, O. 1995 Effort de reproduction chez les oiseaux longévifs: fréquence de reproduction et condition physique chez les pétrels. PhD thesis, Université François Rabelais, France.

Cheverud, J. M., Dow, M. M. & Leutenegger, W. 1985 The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* **39**, 1335–1351.

Cousins, K. & Cooper, J. 1999 The population biology of the black-footed albatross in relation to mortality caused by longline fishing. *Rep. West. Pacific Regional Fish. Mngmt Council*, pp. 14–19 and 37–57.

Croxall, J. P. & Rothery, P. 1991 The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. In *Bird population studies: relevance to conservation and management* (ed. C. Perrins, J.-D. Lebreton & G. J. Hiros), pp. 272–296. Oxford University Press.

Del Hoyo, J., Elliott, A. & Sargatal, J. 1992 *Handbook of the birds of the world*, vol. 1. Barcelona, Spain: Lynx Editions.

Dunham, A. E. & Miles, D. 1992 Comparative analyses of

phylogenetic effects in the life-history patterns of iguanid reptiles. *Am. Nat.* **139**, 848–869.

Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.

Fisher, H. 1975 Mortality and survival in the laysan albatross *Diomedea immutabilis*. *Pacific Sci.* **29**, 279–300.

Fressanges du Bost, D. & Ségonzac, M. 1976 Note complémentaire sur le cycle reproducteur du grand albatros (*Diomedea exulans*) de l'île de la Possession, archipel Crozet. *Commun. Nat. Franç. Rech. Antarct.* **40**, 53–60.

Frings, H. & Frings, M. 1961 Some biometric studies on the albatrosses of Midway Atoll. *Condor* **63**, 304–312.

Gaillard, J. M., Pontier, D., Allainé, D., Lebreton, J. D., Trouvilliez, J. & Clobert, J. 1989 An analysis of demographic tactics in birds and mammals. *Oikos* **56**, 59–76.

Garland Jr, T. & Ives, A. R. 2000 Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* **155**, 346–364.

Garland Jr, T., Midford, P. E. & Ives, A. R. 1999 An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral states. *Am. Zool.* **39**, 374–388.

Gould, P. J. & Hobbs, R. 1993 Population dynamics of the laysan and other albatrosses in the North Pacific. *North Pacific Commun. Bull.* **53**, 485–497.

Harris, M. P. 1973 The biology of the waved albatross *Diomedea irrorata* of Hood Island, Galapagos. *Ibis* **115**, 483–510.

Jouventin, P. & Mougin, J. L. 1981 Les stratégies adaptatives des oiseaux de mer. *Revue d'Ecologie Terre & Vie* **35**, 217–272.

Jouventin, P. & Weimerskirch, H. 1988 Demographic strategies of southern albatrosses. *Proc. of XIX Int. Ornithol. Congr.* **19**, 857–865.

Jouventin, P. & Weimerskirch, H. 1990 Satellite tracking of wandering albatrosses. *Nature* **343**, 746–748.

- Jouventin, P. & Weimerskirch, H. 1991 Changes in the population size and demography of southern seabirds: management implications. In *Bird population studies: relevance to conservation and management* (ed. C. Perrins, J.-D. Lebreton & G. J. Hiros), pp. 297–314. Oxford University Press.
- Jouventin, P., Roux, J.-P., Stahl, J.-C. & Weimerskirch, H. 1983 Biologie et fréquence de reproduction chez l'albatros à bec jaune (*Diomedea chlororhynchos*). *Gerfaut* **73**, 161–171.
- Jouventin, P., Stahl, J. C., Weimerskirch, H. & Mougin, J. L. 1984 The seabirds of the French Subantarctic Islands and Adelie Land, their status and conservation. ICBP technical publication. Status and conservation of the world seabirds, vol. 2, pp. 609–625. Cambridge, UK.
- Jouventin, P., Martinez, J. & Roux, J.-P. 1989 Breeding biology and current status of the Amsterdam Island albatross *Diomedea amsterdamensis*. *Ibis* **131**, 171–182.
- Lack, D. 1968 *Ecological adaptations for breeding in birds*. London: Methuen.
- Marchant, S. & Higgins, P. J. 1990 *Handbook of Australian, New Zealand and Antarctic birds*, vol. 1. Melbourne, Australia: Oxford University Press.
- Myers, R. H. 1990 *Classical and modern regression with applications*, 2nd edn. Boston, MA: PWS Kent.
- Nelson, J. B. 1968 *Galapagos: island of birds*. London: Longmans.
- Nunn, G. B., Cooper, J., Jouventin, P., Robertson, C. J. R. & Robertson, G. G. 1996 Evolutionary relationships among extant albatrosses (Procellariiformes: Diomedidae) established from complete cytochrome-*b* gene sequences. *Auk* **113**, 784–801.
- Petratis, P. S., Dunham, A. E. & Niewiarowski, P. H. 1996 Inferring multiple causality: the limitations of path analysis. *Funct. Ecol.* **10**, 421–431.
- Price, T. 1997 Correlated evolution and independent contrasts. *Phil. Trans. R. Soc. Lond. B* **352**, 519–529. (DOI 10.1098/rstb.1997.0036.)
- Prince, P. A., Rothery, P., Croxall, J. P. & Wood, A. G. 1994 Population dynamics of black-browed and grey-headed albatrosses *Diomedea melanophrys* and *Diomedea chrysostoma* at Bird Island, South Georgia. *Ibis* **136**, 50–71.
- Reznick, D. 1985 Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**, 257–267.
- Rice, D. W. & Kenyon, K. W. 1962 Breeding cycles and behavior of Laysan and black-footed albatrosses. *Auk* **79**, 517–567.
- Saether, B. E. 1988 Pattern of covariation between life-history traits of European birds. *Nature* **331**, 616–617.
- Sagar, P. M. & Warham, J. 1993 A long-lived southern Buller's mollymauwk *Diomedea bulleri bulleri* with a small egg. *Notornis* **40**, 303–304.
- Sagar, P. M. & Warham, J. 1998 Breeding biology of southern Buller's albatrosses at the Snares, New Zealand. In *The albatross biology and conservation* (ed. G. Robertson & R. Gales), pp. 92–98. Chipping Norton, UK: Beatty and Sons.
- Sagar, P. M. & Weimerskirch, H. 1996 Satellite tracking of southern Buller's albatrosses from the Snares, New Zealand. *Condor* **98**, 649–652.
- SAS Institute Inc 1990 *SAS user's guide, statistics*. Cary, NC: SAS Institute, Inc.
- Serventy, D. L. & Curry, P. J. 1983 Observations on colony size, breeding success, recruitment and intercolony dispersal of short-tailed shearwater *Puffinus tenuirostris* over a 30 year period. *Emu* **84**, 71–79.
- Stahl, J.-C. 1983 Habitats d'alimentation et stratégies d'exploitation des ressources des oiseaux marins dans le secteur des îles Crozet (Terres australes et antarctiques françaises). PhD thesis, Université des Sciences et Techniques du Langue-doc, France.
- Stearns, S. C. 1992 *The evolution of life histories*. New York: Oxford University Press.
- Tickell, W. L. N. 1968 The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora*. In *Antarctic bird studies* (ed. O. L. Austin Jr), pp. 1–55. Washington, DC: American Geophysical Union.
- Tickell, W. L. N. 2000 *Albatrosses*. Sussex, UK: Pica Press.
- Tickell, W. L. N. & Pinder, R. 1967 Breeding frequency in the albatrosses *Diomedea melanophrys* and *D. chrysostoma*. *Nature* **213**, 315–316.
- Warham, J. 1990 *The petrels, their ecology and breeding systems*. London: Academic.
- Weimerskirch, H. 1992 Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos* **64**, 464–473.
- Weimerskirch, H. 1995 Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia* **102**, 37–43.
- Weimerskirch, H. 1998 Foraging strategies of Indian Ocean albatrosses and their relationships with fisheries. In *The albatross biology and conservation* (ed. G. Robertson & R. Gales), pp. 168–179. Chipping Norton, UK: Beatty and Sons.
- Weimerskirch, H. 1999 The role of body condition on breeding and foraging decisions in albatrosses and petrels. *Proc. XXII Int. Ornithol. Congr.* **22**, 1178–1189.
- Weimerskirch, H. & Jouventin, P. 1987 Population dynamics in the wandering albatross, *Diomedea exulans*, of the Crozet Island: causes and consequences of the population decline. *Oikos* **49**, 315–322.
- Weimerskirch, H., Clobert, J. & Jouventin, P. 1987 Survival in five southern albatrosses and its relationship with their life history. *J. Anim. Ecol.* **56**, 1043–1055.
- Weimerskirch, H., Bartle, J. A., Jouventin, P. & Stahl, J. C. 1988 Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor* **90**, 214–219.
- Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. 1993 Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* **110**, 325–342.
- Weimerskirch, H., Guionnet, T., Shaffer, S. A. & Costa, D. P. 2000 Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc. R. Soc. Lond. B* **267**, 1869–1874. (DOI 10.1098/rspb.2000.1223.)

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